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FUNCTIONAL TRAITS IN AGROECOLOGY: REVIEW

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A revised trait-based framework for agroecosystems including decision rules

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Abstract

1. Designing agroecological cropping systems, which have enhanced biodiversity and that improve agroecosystem services, is recognized as the most likely method of improving the environmental sustainability of agriculture. However, tools and methods for designing such systems are lacking.
2. To help to fill this gap, we propose a revised trait-based response/effect framework as applied to agroecosystems, which takes into account farmers' decision rules.
3. The framework consists of a "Biophysical module", which describes the biophysical functioning of the agroecosystem on a response/effect traits basis and a "Decision module", which encompasses the farmer's choices that follow decision rules, to account for the high degree of human control of filters and community structure operating in cultivated systems.
4. The introduction of the Decision module and its interactions with the Biophysical module opens new research priorities related to trade-offs between services, to species choice and to the relationships between the community composition, functional structure and the functions.
5. *Synthesis and applications*. We proposed a revised trait-based response/effect framework as applied to agroecosystems, which incorporates farmers' decisions. This framework has great potential to address questions related to the strategic choices associated with multispecies cropping system design, from plant (species choices) to community (optimization of community composition) scales. It also contributes to improving the rationale to manage multifunctional agroecosystems, which extend beyond yield alone, by enabling the exploration of trade-offs between ecosystem services.

KEYWORDS
agroecology, community composition, cropping systems, ecosystem services, farmers' decisions, functional traits, response-effect framework, species choice, strategic choices, technical practices

1 | INTRODUCTION

There are serious concerns about the environmental sustainability of intensive agriculture, which drive a need to turn to more efficient and resilient agricultural systems that would provide enough food with reduced dependency on artificial inputs (pesticides, fertilizers, fuel) (see IAASTD 2009; Koohafkan, Altieri, & Gimenez, 2012; Pretty & Bharucha, 2014). Such systems should result from an agroecological engineering, aiming at modifying agricultural systems, based on ecological principles (Lescourret et al., 2015). They should rely on high levels of biodiversity necessary to ensure proper ecological functions and sustain services other than those pertaining to production and to mitigate dis-services from agriculture[1] (Altieri, 1999; Koohafkan et al., 2012; Malezieux, 2012; Vandermeer, 1989; Zhang et al., 2007). A planned biodiversity, the biodiversity associated with the crops and livestock purposely included in the agroecosystem by the farmer (Altieri, 1999), chosen for species' known characteristics or properties, is thus increasingly introduced into agroecosystems.

In parallel, a decrease in chemical inputs will inevitably lead to an increase in spontaneous biodiversity,[2] which also has its own functions in the agroecosystem (Figure 1a; Altieri, 1999). This spontaneous biodiversity could have detrimental or beneficial effects on the system (e.g. competition with the planned species and supply of services complementary to those related to the planned species respectively), depending on species and situations. Designing and managing such complex agroecosystems requires well-reasoned choices of planned species composition, taking into account biotic interactions, spatial arrangement and technical practices that lead to desirable compromises among the services delivered by the plant community, among which production remains central (Gaba et al., 2015; Rapidel et al., 2015). The tools and methods classically used to design cropping systems, e.g. crop models and factorial experiments, reach their limits in the context of such multispecies agroecological systems mainly because of the difficulties to (1) predict emerging properties of a multi-species cover from the properties of a monoculture, (2) deal with the diversity of species and spatial and temporal arrangements that could be used to establish the crop (Malézieux et al., 2009), thus calling for new approaches to address these crucial issues for next generation agricultural systems.

Trait-based approaches (TBA hereafter), originally developed in the field of comparative functional ecology, have a strong potential to tackle some of the issues raised above (Damour, Garnier, Navas, Dorel, & Risede, 2015; Gaba et al., 2015; Garnier & Navas, 2012; Martin & Isaac, 2015; Wood et al., 2015). Traits, which are morphological, anatomical, physiological or phenological features measurable at the individual level (Violle et al., 2007), are used as proxies for the functioning of organisms. Trait-based approaches (TBA) make it possible to compare and contrast species or cultivars based on well-established traits that are critical for plant performance and plant functions in the agroecosystem, and in turn, make predictions regarding short- and long-term dynamics and functions within and among communities comprised of different trait values. Comparisons of trait values among species and communities have improved the understanding of species distribution world-wide, community assembly rules (which describe species response to the environment and determine which species coexist in a specific habitat) and how organisms affect ecosystem functioning (Figure 2) (see Garnier, Navas, & Grigulis, 2016). This has been encapsulated into the trait-based response/effect framework initially proposed by Lavorel and Garnier (2002) (Figure 1b), and further developed by Diaz et al. (2007) and

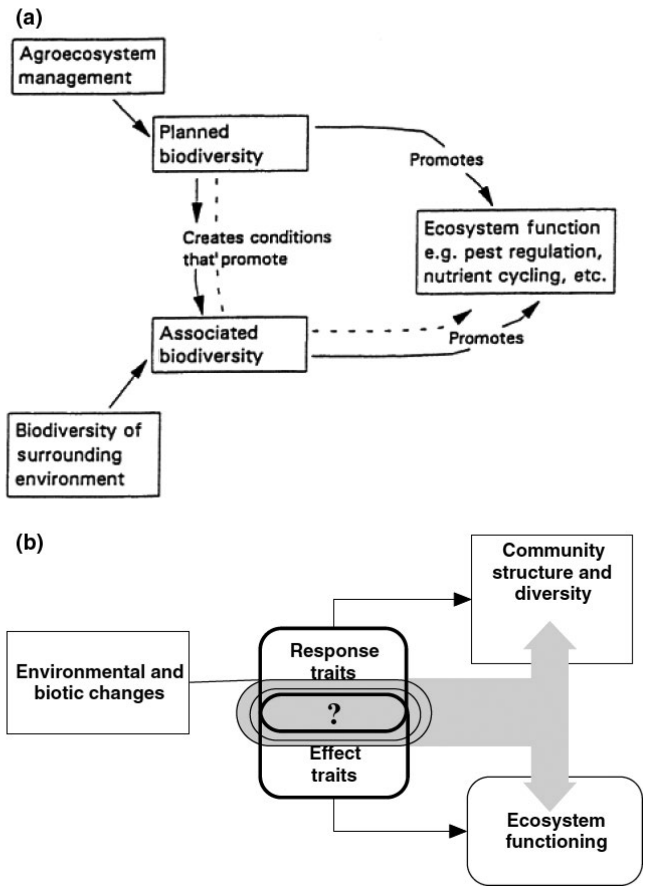


FIGURE 1 (a) Relationships between planned biodiversity and "associated" biodiversity (called spontaneous biodiversity in our text) and ecosystem functions (Altieri, 1999), (b) and the trait-based response/effect framework developed for ecosystems (Lavorel & Garnier, 2002). We prefer to use "spontaneous" instead of "associated" as this last wording could mean, for agronomists, crops that are cultivated in association with a main crop, which is not the meaning we intended. Figure from Altieri (1999) reproduced with permission from Elsevier

Suding et al. (2008). This framework postulates that (1) assembly processes resulting from the action of biotic and abiotic filters sort species according to the values of their response traits, which results in a specific local community functional structure (defined as the distribution of trait values within the community) and (2) in turn, this functional structure affects ecosystem processes and services, according to plant effect trait values (de Bello et al., 2010; de Chazal, Quetier, Lavorel, & Van Doorn, 2008; Diaz et al., 2007; Enquist et al., 2015; Garnier et al., 2016; Kremen, 2005; Lavorel et al., 2011). In this article, we evaluate how this framework could be adapted to agroecosystems, in order to understand how field management, as well as biotic and abiotic filters, shape the plant community composed of both planned and spontaneous species, and how these affect the services delivered.

Although traits have long been used in crop breeding to select cultivars according to their production potential or their tolerance to abiotic stress (Evans, 1993; Gifford, Thorne, Hitz, & Giaquinta, 1984; Murphy, 2007), the interest for TBA to manage community

[1]Agriculture brings a set of benefits and damage, defined as services and dis-services to and from agriculture (Zhang, Ricketts, Kremen, Carney, & Swinton, 2007). In this article, we use "services" to refer both to services and dis-services for the sake of conciseness.

[2]"Spontaneous" species used here are embedded in "associated" species in Altieri (1999). As for agronomists, "associated" species could refer to crops grown in association with a main crop, we prefer to use the term "spontaneous" to avoid any confusion.

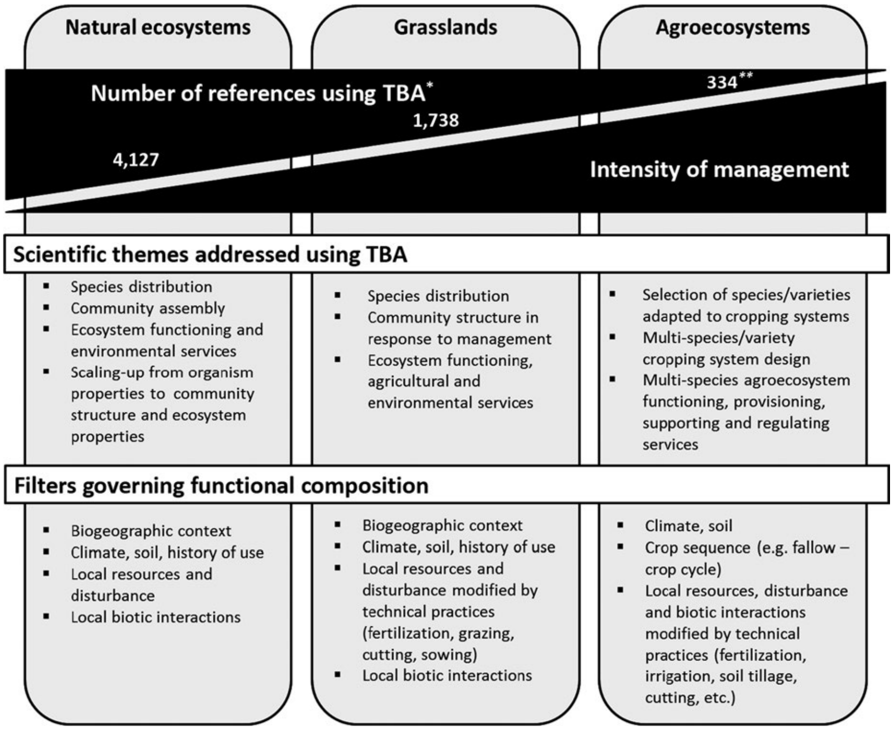


FIGURE 2 The use of trait-based approaches (TBA) in three types of systems arrayed according to their level of management. Grasslands are defined as either natural or cultivated vegetated lands grazed or with the potential to be grazed (see Allen et al. 2004). Here, we excluded fallow fields from "grasslands", even if they can be temporary grazed, because we consider them as an intrinsic component of rotational cropping systems. While grasslands can range from very little managed systems with spontaneous vegetation (close to natural ecosystems) to intensely managed systems with cultivated vegetation (sometimes more strongly managed than some agroecosystems), we assume that most of them are characterized by an intermediary level of management between natural ecosystems and agroecosystems. The number of published references* in which TBA are used decreases with the level of management of the system. The middle part of the figure gives a coarse overview of selected scientific themes which have been addressed using TBA in these systems, while the bottom of the figure lists the main types of filters acting on the three types of systems (see Figure 3 and text for further details). *Results of a literature survey conducted within the *Web of Science* (*WOS*) *Core collection* database on all peer-reviewed articles, book chapters and conference proceedings published between January 2000 and mid-April 2017 containing the terms ("functional trait", "plant trait", "crop trait", "trait-based" or "functional type") and ("plant", "vegetation", crop" or "cultivar") in the *WOS* categories "Biodiversity conservation", "Ecology", "Environmental Sciences", "Environmental Studies", "Forestry", "Multidisciplinary Science", "Plant Sciences" or "Water Resources" for ecosystem analysis, and "Agricultural Engineering", "Agricultural Multisdisciplinary", "Agronomy" or "Horticulture for agrosystems analysis. Grassland analysis was performed on articles containing the terms "herbage", "grassland", "pasture", "meadow", "grasses" in all the *WOS* categories mentioned above. **among these 334 references, 67 deal with weeds

composition in agroecosystems is rather recent and remains relatively limited (Garnier & Navas, 2012; Wood et al., 2015) (Figure 2). For example, a review of the published literature indicates that TBA have been widely used in natural ecosystem, and to a lesser extent in grassland systems; however, there is over an order of magnitude fewer studies employing TBA in agroecosystem (Figure 2), showing that these have been used more extensively in natural ecosystems than in grasslands, and, in turn, more in grasslands than in crops. The current little use of TBA in agricultural contexts is certainly due to the high artificiality of agroecosystems, which requires a shift in perspective to apply these approaches in such settings. This little use is reflected by the absence of a consolidated database of functional traits of planned plants (Martin & Isaac, 2015).

In addition, transferring and adapting TBA to agricultural systems requires taking into account farmer's decision-making, which involves considering: (1) the farmer's control over community structure through the choice of planned species and their spatial organization, (2) the high degree of control of environmental filters via technical practices and (3) a shift in the relative importance of services considered, to account for the greater share of agricultural production in agroecosystems. The aim of this article is to propose a revised trait-based response/effect framework as applied to agroecosystems, which takes into account farmer's decision rules, and help identifying how functional traits might be integrated into decision making. Research priorities in relation to this modified framework are identified. As a first step to articulate these different components, this framework applies at the field scale and deals with primary producers. Potential extensions to other trophic levels (cf. Wood et al., 2015) and larger spatial scales (cf. Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005) are discussed in section 4 below.

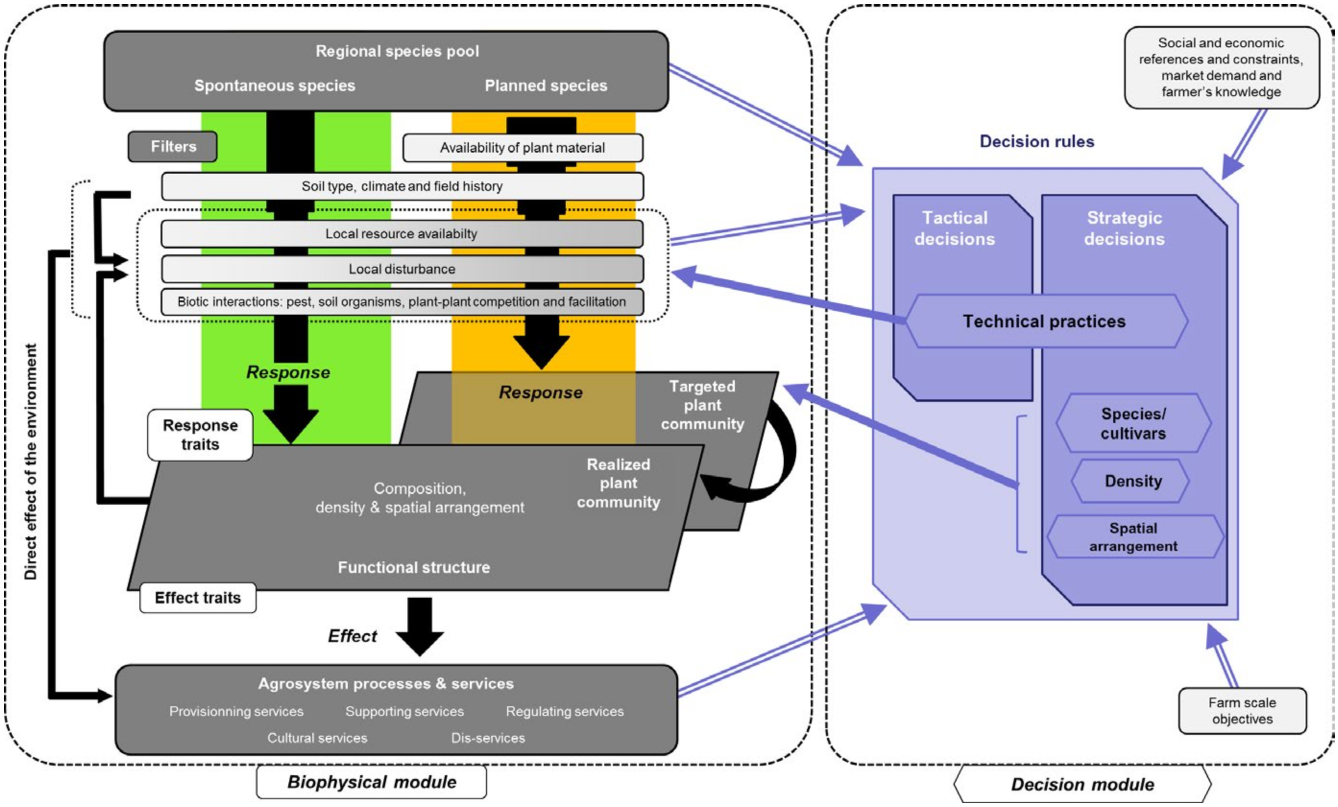


FIGURE 3 The revised trait-based framework proposed for agroecosystems. The revised framework differs from Lavorel and Garnier's proposal (Figure b) by the inclusion of both spontaneous and planned species in the Biophysical module (left part, green and orange boxes respectively) and the addition of a Decision module (right part). The biophysical module and the decision module are in interaction. Drivers of decisions are represented by double violet arrows to decision rules. Impacts of farmer's choices on components of the biophysical module are represented by bold violet arrows from decision rules. Dark grey boxes represent the basic components of the framework. Light grey boxes represent the filters acting on species. Shades of grey reflect that the level of control of filters by technical practices may be sensed differently by spontaneous and planned species. Violet hexagons represent farmers' choices [Colour figure can be viewed at wileyonlinelibrary.com]

2 | A TRAIT-BASED FRAMEWORK FOR AGROECOSYSTEMS

The revised framework applies to the plant community at the field scale, without explicitly considering hedgerows and margins. It articulates Altieri's representation of planned and spontaneous biodiversity in managed agroecosystem (Figure 1a; Altieri, 1999) with the initial response/effect framework of Lavorel and Garnier (2002) (Figure 1b). It consists in a "Biophysical" and a "Decision" modules (Figure 3). The Biophysical module which is partially inherited from the initial framework (Figure 1b), describes the biophysical functioning of the agroecosystem (i.e. the processes that occur in the agroecosystem and involve organisms, e.g. resource acquisition and use, organic matter mineralization, plant–pest interactions, among other processes, e.g. Le Gal, Merot, Moulin, Navarrete, & Wery, 2010) on a response/effect traits basis. This module is further developed to account for the fact that spontaneous and planned species (Altieri's representation, Figure 1a) are subject to different types and degrees of controls (Figure 3). Planned species are those actually managed by farmers who highly control them, while spontaneous species generally receive less attention. The "Decision module" encompasses the farmer's choices that follow decision rules to account for the high degree of control of filters and community structure operating in cultivated systems (Figure 3). This new module corresponds to the "Agroecosystem Management" in Altieri's representation of agroecosystem functioning (Figure 1a). Our revised framework can be applied to a large range of systems, from systems with little degree of control such as natural grasslands or spontaneous fallow (green box of Figure 3) to intensive cropping systems based on the cultivation of one highly controlled crop (orange box of Figure 3), through multispecies agroecological systems which mix several crops and spontaneous species (both parts of Figure 3). In these different contexts, this framework could be used as a guide to design communities that deliver a multitude of desired services.

2.1 | The biophysical module

Planned and spontaneous species may co-occur in a given field, but while spontaneous species arrive and persist according to their response to local filters (Keddy, 1992) (Figure 3, green box), planned species are chosen by farmers, according to their known or assumed suitability for providing certain services under certain environmental

BOX 1 Drivers of decision rules in the context of trait-based approaches in agroecosystems

A general description of the drivers is given in italics, while this description in a trait-based context is given in plain text.

Farmer's decision-making processes are complex and have been extensively studied for the last 30 years (Aubry & Michel-Dounias, 2006; Aubry et al., 1998; Cerf & Sébilllote, 1988; Darré, Mathieu & Lasseur, 2007; Duru, Papy, & Soler, 1988; Le Gal et al., 2010; Papy, 2001; Robert et al., 2016; Sébilllote & Soler, 1990). In the context of the framework proposed here, we grouped decision-making drivers into five groups, described below. These drivers are not hierarchically presented, as the hierarchy, if any, would depend on each situation and is expected to be different for strategic and tactical decisions. Such an analysis is out of the scope of this article.

1. Biological drivers

General: the choice of species and cultivars can only be made in a bounded pool of biodiversity (which may evolve under natural or artificial selection: e.g. Murphy, 2007).

In a trait-based context: the pool, which is defined at a regional scale, is considered not only through the lens of taxonomy and genetics, but also on a functional basis, i.e. taking trait values (mean, range) into account.

2. Environmental drivers

General: climate conditions, soil physical and chemical status and soil topology determine the choice of species (species able to grow or species farmers accept to grow in these conditions) and the choice of the technical practices that would optimize plant growth and development.

In a trait-based context: the value of species/cultivars response traits to the environmental conditions is considered to (1) choose plants adapted to these conditions (strategic decisions), (2) manipulate environmental conditions by technical practices so that the filters acting on the plant community correspond to optimum range of values of response traits of species/cultivars to these filters (tactical decisions).

3. Bundles of services and service trade-off drivers

General: Decision rules should be constructed to provide desirable compromises among the services resulting from the community properties. Trade-off analysis can thus be conducted to determine "service gaps", i.e. the gaps between the potential and the actual level of the service (Rapidel et al., 2015).

In a trait-based context: bundles of services and trade-offs among services are assumed to depend on the functional structure of communities (cf Garnier et al., 2016), and specifically on the distribution of effect trait values in these communities (Lavorel & Grigulis, 2012; Le Roux et al., 2009; Storkey et al., 2015).

4. Farm-scale drivers

General: farm-scale objectives constrain decision rules at a field scale (e.g. organization of working time, working force and materials, crop rotations, financial choices).

In a trait-based context: the functional structure targeted in a specific field ("alpha functional structure") will depend on and influence the functional structure of the communities of the other fields of the farm (the "beta functional structure" of the whole farm), according to the objectives and constraints of the whole farm.

5. Socio-economic drivers

These are related to market demand, social and economic references and constraints, whose perception is determined by farmer's knowledge, resulting from his/her social and educational environment. A further description of these drivers is out of the scope of this article.

conditions (see "Decision module") (Figure 3, orange box). The upper/lower parts of the figure represent respectively the response/effect parts of the framework. They are described below.

Filters acting on planned and spontaneous species found in agroecosystems are represented in the upper part of the Biophysical module in (Figure 3, light grey boxes). They determine which species are sorted from the regional species pool. This regional pool is composed of spontaneous and planned species able to grow in the regional climatic conditions. For planned species, the availability of plant material is considered as a first filter, which depends on socio-economic constraints and determines which species or cultivars can be planted. The other four filters apply to both types of species and determine conditions for plant growth. These filters are related to soil type, climate and field history (including the preceding crops and their management), local resource availability, local disturbance and biotic interactions (either plant–pest, plant–plant or plant–soil organisms) (see Garnier et al., 2016). According to the nature of their relationship with the ecosystem, these filters can be classified into two groups (Chapin, Matson, & Vitousek, 2011): (1) "state factors", which affect the community without being modified by it (soil type, climate and field history), and (2) "interactive controls", which are in interaction with the community and are affected by the state factors (local resource availability, local disturbance and biotic interactions). In our framework, the interactive controls depend both on state factors and on the nature and the frequency of the technical practices (e.g. resource availability is modified by fertilization and plant–pest interactions are modified by pesticide application), which may affect differently spontaneous and planned species (symbolized by shades of grey on Figure 3): for example, weeding in any tree-crop system is an intense disturbance for the spontaneous community species (namely, weed species), but is less directly impactful on the planned community species.

The lower part of the Biophysical module of the framework represents the effects of the community on agroecosystem processes and services (Figure 3, dark grey boxes). The density and spatial arrangement of planned species are mainly chosen by farmers (see "Decision module"). The density and spatial distribution of spontaneous species are mainly modulated by abiotic filters and interactions with planned species. The functional structure of the community, the distribution of effect trait values in the community, modulates agroecosystem processes and determines the services and disservices delivered (see Enquist et al., 2015; Garnier et al., 2016; for a description of the concepts underlying the functional structure—processes relationships). In addition, these relationships between the functional structure of the community and agroecosystem processes and services are likely to depend on the community density and spatial arrangement (e.g. effects on weed and pest control, Weiner, Griepentrog, & Kristensen, 2001; Ratnadass, Fernandes, Avelino, & Habib, 2012).

2.2 | Decision module

Complex processes underlie farmer's decision-making. Decision rules result from production and service delivery objectives, biophysical constraints, market demand and economic, social and cultural references and constraints related to the farmer's knowledge (Aubry, Papy, & Capillon, 1998; Darré, Mathieu & Lasseur 2007; Le Gal et al., 2010; Robert, Thomas, & Bergez, 2016; Sébilllote & Soler, 1990). Socio-economic drivers of decision-making will not be further detailed in this article. In our framework, biophysical constraints are embodied in filters acting on the plant community (Figure 3, Biophysical module, light grey boxes) and production and service delivery objectives are embodied in the services expected from the agrosystem: market production (provisioning service), nutrient cycling (supporting service), pest and disease control or carbon storage (regulating services), recreational value (cultural services) (Figure 3, Biophysical module, lower box).

Decision rules can be conceptually grouped into two categories, depending on the time-scale at which they operate: "strategic decisions" operate at a year or several year time-scale, while "tactical decisions" operate at shorter time-scales (season/week/day) (e.g. Cittadini, Lubbers, de Ridder, van Keulen, & Claassen, 2008; Le Gal, Dugue, Faure, & Novak, 2011; Ripoche et al., 2011; Robert et al., 2016). Strategic decisions correspond to farmer's objectives (e.g. cultivation of a cover crop to control weeds and improve the nitrogen availability) and encompass species, densities and spatial arrangement choices and the type of management to conduct with technical practices (e.g. the need to manually control a twining plant). These strategic decisions are not independent from one another, and their appropriate combination actually determines the functional structure and the performance of the community. Tactical decisions enable the farmer to reach the objectives fixed by the strategic decisions as modulated by shorter term environmental or socio-economic conditions. They encompass the technical practices that enable the implementation of the strategic decisions (e.g. the timing and frequency of plant control according to its development). They are thus determined by the choices of species, density, spatial arrangement and type of management. They affect the filters that apply to the community.

Box 1 details the general drivers of decision rules, and how these can be framed in the context of a TBA to agroecosystem management. Key strategic decisions include (1) the choice of species and cultivars of planned species as a function of their response and effect trait values, chosen to deliver targeted services and for their response to environmental conditions, and (2) the choice of density and spatial arrangement (e.g. rows, strips, random, etc.), to optimize these services. Tactical decisions will then lead the farmer to determine the technical practices applied to the planned and spontaneous species (Figure 3, violet hexagons), according to its observations and what is known about the response traits of species/cultivars to environmental factors (which result from the combination of local—unmanaged—factors and technical practices). This process, which is described here at the scale of a particular field (within community functional structure, i.e. "alpha diversity"), also applies to other fields of the farm according to the overall farm objectives and constraints. The decision rules are then expanded to the community functional structure among fields, i.e. "beta diversity" of the whole farm).

2.3 | Interaction between biophysical and decision modules

The interactions between the two basic modules of the framework are several fold: (1) decision rules rely on at least three drivers of the Biophysical module (double violet arrows on Figure 3): biological (choice of species/cultivars within a bounded pool of biodiversity), environmental (e.g. soil fertility level, rainfall intensity and repartition) and targeted services, (2) technical practices affect the filters that apply to the community (upper bold violet arrow on Figure 3), (3) and farmer's strategic decisions determine the desirable species/cultivars composition, density and spatial arrangement of the community as well as the type of management (e.g. manual weeding, deep tillage) (lower bold violet arrow on Figure 3). The set of decisions leads to the definition of a targeted plant community (background plan on Figure 3), but the actual community obtained (foreground plan on Figure 3) may differ from this targeted community. This might be due to the actual response of species to the environment at the time of seeding/planting and early growth (e.g. transient soil water deficit, seed predation and community disturbance, or pest damages), and to interactions with spontaneous species. While planned species composition and spatial arrangement (e.g. row vs. mixed intercropping, sensu Malézieux et al., 2009) of the realized community is likely to be similar to the ones of the targeted community, the relative densities of planned species may differ substantially between targeted and realized communities. This is an inevitable consequence of the lower degree of control farmers will be able to exert in multispecies agroecological systems as compared to intensive monocultures.

3 | SPECIFICITIES OF THE FRAMEWORK RELATED TO DECISION RULES

Since the Biophysical module has been extensively used and discussed in ecological studies, we will discuss here how the introduction of a Decision module and its interaction with the Biophysical module raise new questions related to the identification of trade-offs between services, to the choice of species and to relationships between the community functional structure and the functions delivered. We illustrate this discussion with the case of a cereal-tree agroforestry system where tree species aim at improving the nutrient efficiency as compared to simple systems without trees (Box 2).

3.1 | Choice of species and cultivars as a function of plant functional profiles

Plant species or cultivar choices are made according to the five drivers presented in Box 1 and to plant material availability. Species/cultivar role and predicted adaptation to soil and climate conditions can be described by "functional profiles" (sensu Damour, Dorel, Tran Quoc, Meynard, & Risede, 2014), constructed from a combination of effect traits related to the services expected and response traits to environmental conditions. Functional profiles reflect plant strategies of functioning, which are revealed by trait syndromes (i.e. suites of related traits) (Chapin, Autumn, & Pugnaire, 1993), resulting from analyses of positive and negative correlations between traits (e.g. in the case of agroecosystems: Gagliardi, Martin, Virginio, Rapidel, & Isaac, 2015; Tardy, Moreau, Dorel, & Damour, 2015; Tribouillois et al., 2015; Damour, Guérin, & Dorel, 2016; Martin et al., 2017; Tardy, Damour, Dorel, & Moreau, 2017). Species functional profiles and strategies compared to the expectations for the system could help the choice of the best plants, for a specific usage (see illustration in Box 2—point 3). As data from different species and systems accumulate, there is a clear need to assemble a collective, open trait database for subsequent use, constructed to minimize uncertainties in defining functional profiles.

3.1.1 | Trait databases for agroecosystems

While large trait databases have been developed for plant species world-wide, with a key focus on "wild plant species"—or rather, the spontaneous species in our framework—(e.g. Kattge et al., 2011; Kleyer et al., 2008), no coordinated large-scale effort has been made up now to synthesize and centralize trait data of planned species in relation to the specific services targeted in agroecosystems (Martin & Isaac, 2015). An appropriate database should include effect traits related to such services, and should be constructed at the cultivar level and include metadata describing accurately how and where data were gathered to account for intraspecific trait variation (see below) to minimize uncertainties in traits evaluation. The construction of trait databases for planned species should also be accompanied by the definition of standardized protocols for trait measurements, inspired from the ones developed for ecological studies (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013) and adapted to agroecosystem specificities (e.g. spatial and temporal field heterogeneity, traits specific to agroecosystems).

3.1.2 | Dealing with intraspecific trait variability

Recent works have emphasized the importance of accounting for intraspecific trait variability (ITV) in both spontaneous and planned species (e.g. Albert et al., 2012; Gagliardi et al., 2015; Kazakou et al., 2014; Martin et al., 2017; Violle et al., 2012). Agroecosystems are the place of intense and frequent disturbances generated by technical practices and are characterized by field-specific management strategies and history resulting in large temporal variations in physicochemical and biological conditions. These variations are likely to affect plant trait values and result in high ITV through both space and time (see illustration in Box 2—point 3). This high ITV could impair our ability to predict ecosystem services from effect trait measurements conducted at a single point in time during the growing season. Beyond the identification of situations in which ITV should be taken into account (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Damour et al., 2015; Wood et al., 2015), these studies suggest adapting the protocols for trait measurements e.g. to account for interindividual variability (Violle et al., 2012), to assess "environmental associations" (i.e. the range of environmental conditions where a particular species/population strives, Garnier et al., 2017), and to use specific methods of data analysis to compare intraspecific and interspecific variability of traits (variance partitioning and T-statistics, respectively de Bello et al., 2011; Violle et al., 2012).

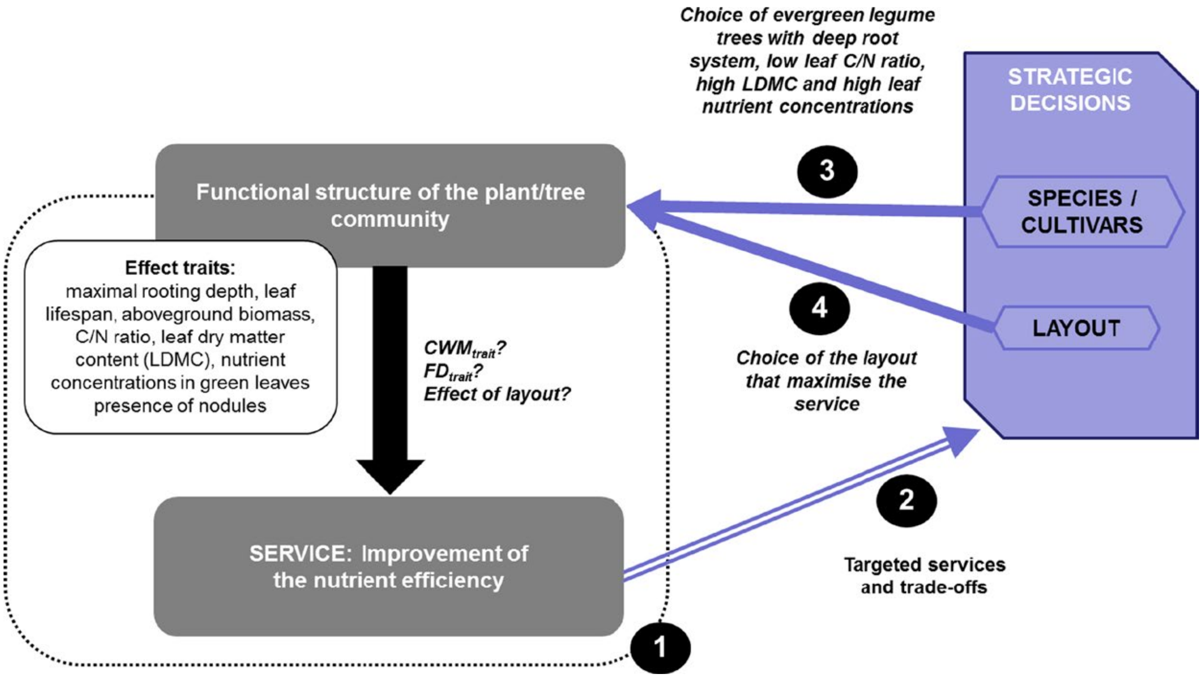
3.2 | Functional structure of the plant community in agroecosystems

The set of decision rules followed will lead to the establishment of a specific functional structure of the plant community, from which the targeted services are expected. These relationships between the community functional structure and the services delivered by agroecosystems raise questions about the nature of these relationships and on the roles of the community density and spatial arrangement.

3.2.1 | Relationships between diversity and agroecosystem properties

One of the central tenets of the response/effect framework is the assumption that the functional structure of the community influence ecosystems properties and the services these deliver. Different metrics describing the functional structure of the community have been used to evaluate these relationships, corresponding to two complementary facets. The first is the community-weighted average trait value (CWM), which accounts for the dominance (or "mass ratio") hypothesis (trait values of species affect ecosystem processes in proportion to their local biomass) (Grime, 1998). The second is the distribution of trait values around the mean (i.e. the functional diversity sensu stricto: FD), which accounts for the "niche complementarity

BOX 2 An example of application of the framework to a multispecies agroecological system (cereal-tree agroforestry system) with the aim of choosing the tree species that improve the nutrient efficiency as compared to simple systems without trees. A focus is made on the lower part of the framework shown in Figure 3 only, to illustrate the specificities discussed in section 3 "Specificities of the framework related to decision rules" [Colour figure can be viewed at wileyonlinelibrary.com]



1. In agroforestry systems, improving the efficiency of nutrients could limit nutrient leaching and improve the soil mineral fertility. It can be provided by three main functions: capture of nutrients by the trees in deep soil layers, redistribution of nutrients by plant litter in the zones of the soil other than those in which they were absorbed and atmospheric nitrogen fixation. Nutrient capture in deep soils is mainly related to the *maximal rooting depth* of species. Redistribution of nutrients by litter was related to five main effect traits: *leaf life span* (indicator of the dynamics of litter deposition), *above-ground biomass* (indicator of litter biomass), *C/N ratio of the litter* and *leaf dry mass content* (indicators of the dynamics of litter decomposition and mineralization) and *nutrient concentration in green leaves* (indicator of the litter nutrient concentration) (see Damour et al., 2015 and references herein). Nitrogen fixation can be related to the *presence of nodules*. Whether these functions are more efficient by manipulating community-average (e.g. CWM: community weighted means) or niche complementarity among species (affecting functional diversity *sensu* stricto: FD) is currently unknown (see section 3.2 for details). To test for these effects, CWM and FD of the community calculated with the six quantitative effect traits mentioned above should be related to indicators of nutrient leaching (e.g. concentration of nutrients collected in lysimeters in deep soil layers) and improvement of nutrient fertility (e.g. concentration of nutrients in the zone of soil explored by half of the roots).
2. Strategic decisions are determined by the five drivers presented in Box 1, among which the search for improving the nutrient efficiency. If other services are targeted (e.g. weed control), strategic decisions should favour the more desirable compromise among services. Trade-offs between improvement of the nutrient efficiency and other services could be suggested by negative correlations between the traits associated to each of these services.
3. Tree species choices are made according to their functional profiles. We assume that evergreen legume trees with deep root system, low leaf C/N ratio, high LDMC and high leaf nutrient concentrations maximize deep capture of nutrients, redistribution of nutrients by plant litter and atmospheric nitrogen fixation. While little intraspecific trait variability (ITV) is usually observed for LDMC, leaf chemical traits (e.g. nutrient concentration and C/N ratio) and root traits (e.g. maximal rooting depth) are recognized to respond strongly to environmental factors (e.g. nutrient and water availability for leaf chemical traits and soil compaction and moisture for root traits) (Kazakou et al., 2014; Lynch & Wojciechowski, 2015; Vocanson, Roger-Estrade, Boizard, & Jeuffroy, 2006). These different ITV of traits should deserve attention when collecting data (cf. Kazakou et al., 2014) (see text).
4. The choices of tree density and spatial arrangement may affect the relationship between the functional structure of the community and nutrient efficiency. Although such relationships have not been established quantitatively, we could expect that a homogeneous repartition of deep rooted trees will maximize deep capture of nutrient (and nutrient leaching limitation) and provide a homogenous redistribution of nutrients in the field. Row agroforestry systems (Malézieux et al., 2009) is likely to maximize these functions, while allowing for managing the distance between rows so as to provide cereal crop with sufficient light.

hypothesis" (ecosystem processes depend on the presence of species which use resources in a complementary manner) (e.g. Petchey & Gaston, 2006) (see illustration in Box 2—point 1). A recent literature survey tends to demonstrate that in studies that have tested simultaneously both hypothesis, dominance effects have been detected more frequently than complementarity effects (reviewed in Garnier et al., 2016; Lavorel, 2013). Which facet(s) of community functional structure best relate to ecosystem properties remains an open question however, not only in agroecosystems but also in more natural ecosystems.

3.2.2 | The impacts of community density and spatial arrangement

Whether and how the density and the spatial arrangement of plants affect the relationships between the functional structure of the community and agroecosystem processes is a question which has been incompletely addressed. While the roles of crop spatial arrangement (e.g. Ratnadass et al., 2012) and plant density (from theoretical analysis, Damour et al., 2015) on important agroecosystem processes have been shown (see hypothesis in the illustration of Box 2—point 4), knowledge, methods and theory to scale-up from the individual plant traits to the community level commonly developed for natural ecosystems (Garnier et al., 2004; Lavorel, 2013; Lavorel et al., 2008; Shipley, Vile, & Garnier, 2006) have not explicitly incorporated information on species-specific density and spatial arrangement (Damour et al., 2015). Metrics of community functional structure that account for the effects of density and plant spatial arrangement have to be designed (expressing community functional structure on a soil area basis, integrating plant spatial arrangement, etc.) (Damour et al., 2015). Recent attempts for linking spatial patterns of functional diversity to assembly processes in ecosystems using spatial autocorrelation analysis have been made (e.g. Biswas, Mallik, Braithwaite, & Wagner, 2016). The benefits of such methods for describing patterns of agroecosystem spatial arrangements and how these patterns affect ecosystem properties need to be assessed.

3.3 | Multifunctionality of agroecosystems and bundles of services

The concept of multifunctionality in agriculture underlines the fact that agriculture produces jointly commodity outputs (food, fuel and fibre) and non-commodity outputs like climate change mitigation, biodiversity and landscape conservation or rural viability (OECD 2001; Renting et al., 2009). These outputs are considered as services provided by agroecosystems (Zhang et al., 2007). Here, a key issue is to identify so-called "bundles of services", which are sets of services that appear together repeatedly (Raudsepp-Hearne, Peterson, & Bennett, 2010). Those that covary positively suggest synergies among services, while those that covary negatively suggest trade-offs. While synergies between intended services should be actively stimulated, "trade-offs" should be analysed and anticipated to favour the most desirable ones.

These trade-offs are considered at two stages in our framework: (1) during the definition of the farmer's objectives, which can result in a choice favouring one service at the expense of the other (e.g. choosing a cover crop that strongly control weeds, while providing only little improvement of nitrogen availability), and (2) during the actual phase of cultivation, when the functional properties of the community may lead to undesired levels of certain sets of functions, which may possibly be corrected using relevant technical practices (e.g. mowing a vigorous cover crop that efficiently controls weeds but is competing with the main crop). As a consequence, the knowledge of trade-offs between services is a key lever for agroecosystem design and management, and enables the optimization of the performances of the system. The importance of the analysis of trade-off between services in agroecosystem studies has been shown and have been proposed as a tool to assess "service gaps", i.e. the gaps between the potential and the actual level of the service (inspired from the concept of yield gap, see van Ittersum & Cassman, 2013) (Rapidel et al., 2015).

Trait-based approaches (TBA) provide a general representation of the effects of management on community functional structure. Given that a number of ecosystem properties have been shown to relate to this structure, TBA can be used to manage multiple ecosystem services simultaneously (Wood et al., 2015). More precisely, by relating the functional structure of the community to the services delivered, the revised trait-based framework we propose enables the exploration of their trade-offs on the basis of correlations between service-related effect traits (Lavorel & Grigulis, 2012; Le Roux et al., 2009). In turn, this allows one to find desirable compromises among services, which is one driver of decision rules (Box 1—driver 3) (see illustration in Box 2—point 2). Trait-based analyses of service trade-offs in agroecosystems are few, but pioneer studies demonstrate their feasibility and potential (e.g. Storkey et al., 2015). Other recent works also suggested that functional diversity increases the multifunctionality of agrosystems (Finney & Kaye, 2016).

4 | SCOPE OF THE REVISED FRAMEWORK

4.1 | Opportunities for system design and management

Trait-based approaches (TBA) open a large field of applications to agroecological research, from the plant to the global scale (see Martin & Isaac, 2015). The revised framework we propose was designed to understand the response of communities to their environment and their impacts on ecosystem functioning and the resulting services. Such knowledge is essential to the design and management of communities that optimize a set of services and has to be integrated into decision-making. Beyond the fact that many traits are key determinants/inputs in most prominent process-based models (e.g. Brisson et al., 1998; Jones et al., 2003), we argue that functional traits can be used, at least, for three kinds of applications in agroecosystems, according to the literature published so far.

First, several studies have shown the benefits of using functional traits for the selection of species and cultivars. For example, response traits related to shade tolerance have been used to select suitable cover crops in orchards (Mauromicale, Occhipinti, & Mauro, 2010), and response traits related to environmental stress such as drought have been used to choose cultivars well adapted to low rainfall regions (e.g. Annicchiarico, 2007). Knowledge of effect traits affecting agroecosystem services have enabled one to choose cover crops that deliver the expected services, used as in the rotation or associated with the main crop in different types of cropping systems (Damour et al., 2014; Finney & Kaye, 2016; Storkey et al., 2015; Tribouillois et al., 2015; Wilke & Snapp, 2008). Recent modelling approaches based on community functional structure / services relationships have provided tools to define the functional structure, and thus the species composition of community, that deliver desirable compromises among services (Laughlin, 2014; Storkey et al., 2015).

Second, functional traits give a good insight into the response of yield components to management regime and could provide directions for management. This can be illustrated with two recent examples: in coffee agroforestry systems, Gagliardi et al. (2015) have shown that leaf traits related to resource acquisition were negatively correlated with light levels determined by shade management and weakly but significantly with coffee yield components, while in banana cropping systems, Dorel et al. (2016) have shown how traits related to the banana yield were modified by the pruning regime of suckers, in relation to changes in the source-sink ratio.

And third, functional traits can efficiently be used to understand weed community dynamics in relation to technical practices and crop identity and to provide directions for long-term weed management (Fried, Kazakou, & Gaba, 2012; Gunton, Petit, & Gaba, 2011; Trichard, Alignier, Chauvel, & Petit, 2013). These knowledge should enable to shift from weed management method based on chemical applications to less environmentally damaging practices.

4.2 | Beyond plants and single fields

The revised framework presented here is focused at the community level, where TBA have mostly been developed and applied to date. In agroecosystems, it can thus be employed and used to make predictions at the field scale. However, a plant community is in close interaction with the soil community (micro and macro-fauna of decomposers, mineralizers, engineers, pest and parasites) and the aerial community (pest and beneficial micro and macro-fauna). The roles of this network of interactions on biological regulations and services delivered by agroecosystems are increasingly understood (e.g. Ehrmann & Ritz, 2014; Tixier et al., 2013). An improved version of our framework would need to consider interactions with these other trophic levels, as proposed for natural systems by e.g. Lavorel et al. (2013) (see also Wood et al., 2015).

The approach taken here at the field scale should be considered as a first step towards a more general scheme accounting for the spatial organization of farms and landscapes in which these are embedded, which is needed to understand the processes underlying services in agroecosystems (reviewed in Tscharntke et al., 2005). First, fields of a same farm are connected because: (1) they are usually physically close to one another, which implies fluxes of organisms (both spontaneous and planned) among the different fields, (2) the working force and farm equipment is distributed primarily among these fields, and (3) the farmer's overall objectives are determined at the level of the whole farm. A prospect is thus to extend the revised framework to take into account these spatial aspects, which involve the understanding of controls on "beta diversity" (among fields) and how to manage the functional complementarity of the different fields to optimize the delivery of services at the whole farm scale (see Box 1). Second, as some of the services delivered at the field scale are supported by trophic groups that can move within the landscape (e.g. presence of beneficial insects, disease dispersion, pollination, etc.), a comprehensive framework for agroecosystem functioning would need to combine a multiscale with a multitrophic approach.

4.3 | Precision vs. generalization

Duarte, Sandjensen, Nielsen, Enriquez, and Agusti (1995) compared the scope of application of comparative ecology, the field of ecology in which TBA are mostly used, to that of autecology, whose aim is the precise understanding of species resource requirements. These authors argued that the strength of the comparative approach is its capacity for large generalizations, although it may lack in the precision required for the description of detailed, small-scale mechanisms. A comparable analysis holds in the case of TBA as applied to agronomy. While TBA represent a large potential for defining general patterns of plant and agroecosystems functioning, they do not provide us with a precise mechanistic understanding of this system and its components. As a consequence, the revised framework proposed here is not designed to drive tactical decisions—decisions that operate at small time-scales and correspond to the precise management of the system—like dose and timing of fertilization, timing of mowing, sanitary deleafing, etc. Its aim is rather to shape strategic decisions, like species, density and spatial arrangement choices, which underlie the design of the multispecies cropping systems at the basis of the next generation agricultural systems (e.g. Damour et al., 2014; Fried et al., 2012; Storkey et al., 2015).

To conclude, the proposed trait-based response/effect framework that includes farmer's decision-making has considerable potential to help solving questions related to the strategic choices associated with multispecies cropping system design. Further developments of this framework for agroecosystems would involve considering trophic levels other than plants and larger spatial scales, for an improved understanding of service delivery in heterogeneous, large-scale agricultural landscapes.

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AUTHORS' CONTRIBUTIONS

G.D. initiated the project and led the writing with contributions from E.G. and M.L.N. at all stages.

DATA ACCESSIBILITY

Data have not been archived because this article does not use data.

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